

# THE ALIMENTARY CANAL OF MERACANTHA CONTRACTA BEAUV. (TENEBRIONIDÆ).\*

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## INTRODUCTION.

The Tenebrionid beetle, *Meracantha contracta* Beauv., is a medium sized (11-13 mm.), ovate and strongly convex species. It is wingless and especially distinguished by having the head received in the thorax nearly to the eyes. It occurs east of the Mississippi River and is very abundant in the oak and maple forests of the northern part of Ohio.

The problem of making an anatomical study of the alimentary canal of this species was suggested because of the availability of specimens and their interesting bark eating habits. The specimens used for this study were collected at Put-in-Bay, Ohio, from the trees found on the northern border of South Bass Island.

The process of preparation was as follows: The specimens were chloroformed, the elytra cut off and then the abdomens of some slit open dorsally, of others ventrally, before being fixed in Carl's fluid and preserved in 80% alcohol.

Upon dissection of the specimens it was discovered that in many cases an improvement could have been secured by a more extensive opening of the body, especially through the thorax and head. This would have allowed a much quicker penetration of the tissue of the anterior end of the mid-gut and the fore-gut as the heavy chitin surrounding this region slowed down the action of the fixative thus causing some tissue disintegration before complete permeation was reached. The fore-gut especially was very inaccessible, as it was found to be confined to the head and of necessity therefore, extremely short.

Due to the heavy intima of chitin in the fore- and hind-guts, it was found necessary in sectioning to pay particular attention to keeping the edge of the microtome knife sharp as there was a constant tendency for these sections to crush and tear. Most

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of the sections were cut 8 microns in thickness and gave good results in staining.

The ordinary double staining process with Delafield's Hematoxylin and Eosin was used in the preparation of slides.

The drawings were made with the aid of a camera lucida.

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#### GENERAL DESCRIPTION.

Strictly speaking the alimentary canal is a rather simple tube extending from one end of the insect to the other. In the case of the beetle under discussion, which is a phytophagus or plant eater, it is of medium length extending in a nearly median line (Figs. 1-2) from the mouth parts back to the beginning of the abdomen where it curves slightly to the right down as far as the third segment, where it curves to the left and comes up to the first segment close to the edge of the body cavity and near the dorsal surface. It is then angulated and again approaches the median line just anterior to the first segment and then passing over itself in the second and third abdominal segments. It is thus nearly half again as long as the entire body.

*Meracantha contracta*, as is generally true of all insects, has three primary divisions of the alimentary canal present (Fig. 3); the stomodium or fore-gut, the mesenteron or mid-gut and the proctodeum or hind-gut.

The conditions concerning the attachments of the canal in the body are the same as in all insects: the fore-gut and hind-gut are invaginations of the ectoderm and therefore the body wall is, of necessity, continuous with the alimentary canal at both extremities. It is also supported by tracheæ along its entire length, as these support the gonads and fat-body, which in turn form a supporting sheath about the canal. Also there are certain suspensory muscles attached to the dorsal wall.

In origin, the fore-gut and hind-gut, as mentioned in the preceding paragraph, arise as invaginations of the body wall, and thus are ectodermal in origin. The mesenteron, however, has an altogether different history as it is formed by the proliferation of rings of endodermal cells, one around the inner end

of the fore-gut and the other around the inner end of the hind-gut. The endodermal cells form the digestive epithelium and all muscles, tracheæ and connective tissue concerned with the canal are of mesodermal origin.

Thus two important features of the canal will be observed; first, that the fore-gut and hind-gut being ectodermal in origin, resemble the body wall in structure, and second, that the mid-gut being mesodermal in origin, presents a marked difference, histologically, from either the fore-gut or hind-gut.

The gross parts of the canal of *Meracantha contracta*, can be listed as follows:

1. The mouth, the part opening to the exterior, located in the head and concerned with the mouth parts.
2. The pharynx, the region just distal to the mouth.
3. The oesophagus, the first and most simple part of the throat tube.
4. (No crop is evident because of the extreme shortness of the entire fore-gut, which extends only the distance through the head.)
5. The gizzard or proventriculus, the lower end of the oesophagus having a much thickened chitinous intima, thrown into many folds and surrounded by prominent circular muscles.
6. The oesophageal valve (cardiac valve); this is situated at the union of the fore-gut and mid-gut and acts as a valve below the gizzard, preventing regurgitation.
7. The stomach or mid-gut; this is the digestive part of the canal.
8. The pyloric valve; this is located at the union of the mid-gut and hind-gut.
9. The Malpighian tubules; these are six in number and are attached to the canal just posterior to the pyloric valve.
10. The hind-gut; this is the third primary division of the canal and is further subdivided into:
  - A. The small intestine or ileum, the small angulated part of the hind-gut posterior to the pyloric valve.
  - B. The large intestine or colon, the larger and somewhat thinner walled part of the hind-gut posterior to the ileum.
  - C. The rectum, a short funnel-shaped organ, connecting the colon and the exterior of the body.
  - D. The anus, the aperture connecting the rectum and the exterior of the body.

Each of these divisions will be described under the subject, "The Histology of the Canal."

#### THE HISTOLOGY OF THE STRUCTURE OF THE ALIMENTARY CANAL.

##### THE FORE-GUT OR STOMODEUM.

In *Meracantha contracta* this portion of the canal is confined entirely to the region of the head (Fig. 4), the union with the mid-gut taking place at the posterior opening in the head, which is slightly larger than the anterior end of the mid-gut. By actual measurement the fore-gut only averages two millimeters in length.

A longitudinal section through the head discloses that there is a definite adaptation to the bark-eating habit. Below the labrum or upper lip, which is slightly flexible, a pair of strong-toothed mandibles extend well back into the head, where powerful muscles operating

them are attached to the posterior walls. The mandibles work from side to side and each possesses at its posterior end, on the inner surface, a heavily chitinized plate known as a molar or crushing surface. Anterior to these plates are areas of thinner chitin, and from the floor of the mouth, slightly in front of the plates arises a hypo-pharynx or tongue-like structure which is connected with the posterior end of the labrum or lower lip. The posterior part of the mouth cavity is large and narrows down where it joins the anterior end of the fore-gut. (Fig. 4).

The pharynx extends from the mouth cavity to about where the tube is encircled by the large and prominent brain ganglia. The intima of the pharynx as well as that of the rest of the fore-gut, is armed with small backward directed spines, arising from small punctures or invaginations in the intima.

The oesophagus is very short and widens out considerably in a funnel shape before joining the mid-gut. The lower portion of the oesophagus has a prominent thickening of the chitinous intima which is much ridged in nature. This portion is known as the proventriculus or gizzard, (Fig. 6). No evidence of a crop is seen due to the extreme shortness of the fore-gut and probably little or no digestive action occurs while the food is passing through the fore-gut. No evidences of salivary glands were observed. Histologically, as a rule, the following layers, from within outwards, can be recognized. First, the intima or innermost lining, which takes the form of a chitinous layer, directly continuous with the body wall. Second, the epithelial layer, continuous with the hypodermis and chitogenous in function. Third, the basement membrane bounding the outer surface of the epithelium. Fourth, the longitudinal muscles. Fifth, the circular muscles. Sixth, occasionally the peritoneal membrane, a structureless connective tissue composed of very thin cells and difficult of detection.

Examination of a cross section through the fore-gut of *Meracantha contracta*, (Fig. 5) shows a well-developed intima consisting of a thick layer of chitin, armed with spines, the primary cuticula. This is backed by a variable region of chitin, the secondary cuticula. Next to the intima occur the rather large cuboidal epithelial cells. These vary somewhat in size but all contain large oval nuclei densely filled with coarse deep-staining chromatin granules.

The basement membrane is not clearly differentiated, but this is probably due to the action of the fixative. The longitudinal muscles occur within the circular muscles, lying in strands at irregular intervals. They continue throughout the fore-gut and pass on into the mid-gut.

The longitudinal muscles are continuous with the mid-gut and divide into several strands just before reaching the point of extension into the mid-gut. Some of these continue down into the folds of the valves while the rest pass between the circular fibers and cut abruptly across to the surface of the mid-gut where they continue throughout its extremity. (Fig. 6).

The circular muscles are very strongly developed, forming a continuous layer over three times the width of the epithelial tissue. They are clearly striated, with many nuclei present. They appear to have

developed in accordance with the effort required to force the bark particles eaten, down into the proventriculus.

The peritoneal membrane, if present, is not capable of detection.

#### THE UNION OF THE FORE-GUT AND MID-GUT.

At the point of union between the fore-gut and the mid-gut, a structure is present which is known as the oesophageal or cardiac valve. It is formed by a fold of the fore-gut extending down into the mid-gut. This then becomes reflected upon itself and passes forward to unite with the wall of the mid-gut. (Fig. 6).

The histological structure of the valve, discloses that the intima disappears at the end of the fore-gut, where there is a well-marked change in the character of the epithelium. These epithelial cells, in the fold, gradually change from a cuboidal shape into narrower and more elongate cells with their nuclei at the tips, thus they appear at the periphery of the curve in the fold.

Where the intima ceases, the epithelium has assumed the characteristic elongated type of the mid-gut, although there is a marked shortening in a few cells just preceding, due to the abrupt curve and impingement against the circular muscles.

A well-marked ring of circular muscles appears within the interior of the fold, which acts as a sphincter, allowing the valve to be closed.

The longitudinal muscles are represented in the valve by only a few scattered strands extending down from the fore-gut.

The valve appears from a ventral view, as a number of flaps or folds, which when drawn together by the circular muscles, in much the same manner as a meal sack, fit together in such a way as to completely close the orifice and prevent any regurgitation of food. (Fig. 7).

#### THE MID-GUT OR MESENTERON.

This portion of the alimentary canal in *Meracantha* extends from the posterior part of the head to the third abdominal segment where it curves to the left and up to the first segment. (Fig. 3). Its great size in comparison with the rest of the tract is very striking. In addition, the ringed or segmented appearance of the gut is noticeable. This condition is due to the position of the gut circular muscles which are gathered together in bundles at intervals, and cause constrictions in the surface, that appear as rings about the gut.

The longitudinal muscles continue from the fore-gut down the mid-gut, crossing over the union of the two guts in distinctive bundles that give the anterior end of the mid-gut a constricted appearance at intervals. (Fig. 8). These constrictions are at right angles to the circular constrictions. The fibers then diverge and course along the mid-gut crossing the circular muscles at approximately right angles. Thus the whole surface presents a plaid-like appearance. The muscle fibers apparently do not inter-branch to any great extent, but are densely interwoven by very small tracheoles which run throughout the whole surface in very irregular fashion. (Fig. 9). Scattered at frequent intervals between the so-called bundles of circular muscles are isolated circular muscles.

The layers of the wall of the mid-gut are, from the inside out, as follows:

First, the digestive epithelium of endodermal cells.

Second, the basement membrane.

Third, the circular muscles.

Fourth, the longitudinal muscles.

Fifth, the peritoneal membrane which is not discernible in the slides prepared in this study.

The limits of the mid-gut are marked anteriorly by the oesophageal valve and posteriorly by the Malpighian tubules. Examination of a cross section through the mid-gut (Fig. 10) shows the epithelium to be composed of columnar cells, which vary considerably in length, size and shape, probably due to the physiological condition they happen to be in at the time. The majority of the cells however, are long and narrow and contain large median and ovate nuclei densely filled with coarse chromatin granules. Toward the outer margin of the cells, the nuclei gradually fade out. Scattered irregularly along at the bases of the cells are replacement cells pushing up from the nidi or nests of new cells. These cells are somewhat triangular in shape and wedged in between two of the larger cells, which, gorged with digestive secretions, burst into the lumen of the gut. Secretion is thus holocrine as the ruptured ends of the cells indicate. A striated border if present is obliterated by the broken and ruptured ends of the cells, as the insects were fixed at a time when the mid-gut was gorged with food and the process of digestion active.

A peritrophic membrane is present in the lumen, which protects the delicate epithelial tissue from the action of the coarse bark particles. This is probably secreted by the epithelial cells in general as there is no evidence of any specialized cells at the extreme fore end of the gut as found in some insects. In fact the membrane does not make its appearance until some distance back of the anterior end.

The basement membrane is present at certain portions of the cross section and probably would be evident throughout, if the action of the fixative had been quick enough.

Both circular and longitudinal muscles are striated, with numerous nuclei present, and their respective relation to each other in regard to position is the reverse from that found in the fore-gut, namely, the longitudinals being exterior to the circulars. The two layers interchange positions at the oesophageal valve, where the fibers interlace as previously described. (Fig. 6).

The connective tissue containing the muscles and surrounding the exterior of the canal is plainly evident.

No evidence was obtained of any differentiation between digestive and absorptive cells, probably they possess a double function which is characteristic throughout the mid-gut. The digestive epithelium terminates abruptly where the Malpighian tubules enter the canal, being followed immediately by the epithelium of the intestine or hind-gut.

## THE UNION OF THE MID-GUT AND HIND-GUT.

## THE PYLORIC VALVE.

In *Meracantha contracta* there is a definite pyloric valve which however, probably does not function in closing the gut as the fecal matter enclosed within the peritrophic membrane keeps the region of the valve widely distended.

In structure the form of the valve is very similar to the oesophageal valve, although there is not the gradual change in cell structure, (Fig. 11). Enclosed within the fold of cells is a definite group of circular muscles, with a few scattered strands of longitudinal muscles. The intima of the hind-gut where the valve commences, makes a gradual curve into the lumen for a short distance, then a sharp curve folding back upon itself before extending back into the gut, the epithelial cells abruptly shortening. Thus the portion of the wall called the valve is very little thicker than the wall at any other point. There is thus no impediment offered as the fecal matter is forced out of the fore-gut into the hind-gut.

## THE HIND-GUT.

This is called the proctodeum and includes all of the intestine from the stomach or mid-gut to the anus.

Histologically, the layers of the wall of the hind-gut are, from within outwards, as follows:

- First, the intima.
- Second, the epithelium.
- Third, the basement membrane.
- Fourth, the inner circular muscles.
- Fifth, the longitudinal muscle strands.

Sometimes there is present in some insects a layer of outer circular muscles and also a "peritoneal membrane" of connective tissue cells. These last two are lacking in *Meracantha contracta*.

The intima or chitinous lining is secreted by the epithelium which is invaginated body wall and has the same general characteristics as the hypodermis.

The epithelium is identical with the hypodermis of the body wall and is for the most part composed of cuboidal-shaped cells.

The basement membrane is indistinct throughout the hind-gut.

The inner circular muscles are a distinctive layer.

The longitudinal muscles are present and grouped for the most part into large bands.

Three well-marked regions are recognizable in the hind-gut: the small intestine or ileum, the large intestine or colon, and the rectum, (Fig. 3). These will be discussed in order.

## THE ILEUM.

This region comprises about one-third of the total length of the hind-gut and is rather convoluted in the region of the first abdominal segment. It enlarges into the division called the colon at the point where the Malpighian tubules become attached to the surface of the gut.

The primary intima of this region is rather thin but the secondary intima is quite thick. The epithelium is composed of cuboidal-shaped cells and thrown into folds, six seeming to be the average. The cells are distinct in the anterior part of the gut, but tend to become less distinct posteriorly. The nuclei are large and prominent.

The circular muscles are well developed throughout the region. The longitudinal muscles lying outside of the circulars, are scattered at irregular intervals over the ileum.

The basement membrane is indistinct, both throughout the ileum and the colon as well.

#### THE COLON.

There is no abrupt transition, between this region and the one preceding as the epithelium changes gradually in appearance. The primary intima becomes somewhat thicker, with the secondary still very evident.

However, a new set of longitudinal muscles makes its appearance, outside of the circular muscles, being definitely grouped in six bands. These become larger and thicker as they approach the rectum. The spaces between the bands are evenly distributed and each contains a Malpighian tubule. Connective tissue closely holds the Malpighian tubules in place. (Fig. 12).

The circular muscles are well developed at the anterior end of the colon, but gradually disappear until only a few fibers are left near the posterior end.

As the course of the colon is observed towards the rectum, the epithelial cells become more and more flattened, and their boundaries become less distinct. Their protuberances into the lumen of the gut are irregular and give a distinctive wavy appearance to the intima.

#### THE RECTUM.

This region, similar to a cone in appearance, the narrow end terminating in the oval aperture, is characterized chiefly by its very abrupt union with the colon, (Fig. 13). A great enlargement of new circular muscle fibers make their appearance here and probably act as an intestinal valve. The sphincter being thus formed, is much more developed than the one formed at the pyloric valve, hence this probably takes its place in function.

The circular muscles gradually decrease in number and thickness as the oval aperture is approached. The longitudinal muscles disappear entirely.

The intima at first is quite smooth but soon forms many folds which posteriorly become very pronounced, and somewhat tooth-like in appearance. Ordinarily these so-called "teeth" or rectal pads (Fig. 15) are six in number but in the case under discussion there is a marked irregularity. They probably vary in number from four to seven or eight, (Fig. 14).

At the anterior end of the rectum, the intima forms a bulge out into the body cavity. This evidently facilitates the attachment of the muscles of the colon and the origin of those in the rectum as well.



The epithelial cells are much smaller than those in the colon while the divisions between them are more pronounced. The nuclei are relatively large and contain large granular masses.

The chitinous spines as observed in the fore-gut are entirely lacking in the rectum as well as in the hind-gut in general.

#### THE MALPIGHIAN TUBULES.

These vessels are ectodermal in origin and therefore should be associated with the hind-gut. Their function is primarily urinary. Upon sectioning and staining the tubules, deposits of concretions are found scattered throughout the epithelium. These are probably depositions of such end products as uric acid, urates, etc.

In *Meracantha contracta*, the tubules are six in number and originate at the union of the mid-gut and hind-gut, being equally spaced about the gut. From this region of origin, they then course throughout the body cavity in general, winding about the viscera and finally becoming attached to the wall of the hind-gut at the point where the colon commences.

The method of attachment to the colon is very peculiar and worthy of especial notice. The six tubules come together and are much flattened and closely joined together by connective tissue, (Fig. 19) for a distance of about three millimeters before they branch out to course down the sides of the hind-gut. They do not coalesce into a common duct however, as each tubule can be separated out from the band. There is a sharp angulation in the direction the tubules take before they branch out from the band. The whole arrangement is certainly very specialized, and would appear to allow of the ready movements of the colon without bringing undue strain upon the tubules. There is a possibility that it is an adaptation to a special method of defecation. However this point needs further study.

From the points of attachment to the external wall of the colon, each tubule courses in a zig-zag manner down the wall between two bands of longitudinal muscles, (Fig. 20). They are in close contact with the wall of the intestine, being held fast by a thick sheath of connective tissue. As they continue down the colon, they become more compressed in nature and finally terminate blindly just before the beginning of the rectum. (Fig. 21).

The brownish color that is observed in various parts of the tubules is evidently due to the concretions previously mentioned. Near the point of origin they are nearly circular but become more and more flattened as they approach the point of attachment at the colon.

Histologically, it is observed, that they consist mainly of a thick epithelium, with an outer layer of connective tissue. The nuclei are very large, prominent, and filled with coarse granular chromatin. (Figs. 17-18).

Near their origin they contain a prominent lumen and the epithelial cells are densely packed with urinary concretions. Near their blind endings (Fig. 21) however, they become very bead-like in appearance, due to the large turgid epithelial cells, and greatly compressed, the lumen in many instances being barely discernible.

## CONCLUSION.

In conclusion, it is to be noted that in this study of *Mera-cantha contracta*, there is much more to be accomplished before a complete understanding of the alimentary canal can be secured. More species of the Tenebrionidæ should be studied and comparisons drawn as to the adaptations in the canal, for the particular types of food eaten. There is no question that the type studied is very highly specialized. The degree of this specialization should be determined if possible. Also, the specimens studied show a high degree of parasitic infestation in the epithelial tissue of the mid-gut. This parasite is evidently intracellular in nature. In addition, there are present in the fecal material of the hind-gut, many single-celled organisms, obviously of a plant-like nature, possibly yeasts. These occur in great numbers, in strings and singly, in the posterior region of the gut, but are found only sparsely in the anterior region. These should be identified and their effect upon the alimentary canal investigated. In addition the relation of the nature of the bark eaten and the morphological adaptations should be compared. The physiology of the digestive system should be worked out with fresh material in order to understand the anatomical relationships.

In brief, it can readily be seen, therefore, that only a start has been made in this study, and that the pursuit of one problem has opened the need for investigation of many more.

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## EXPLANATION OF PLATES.

## PLATE I.

- FIG. 1. Dorsal view of the abdominal viscera and the portion of the alimentary canal visible.
- FIG. 2. Ventral view of the abdominal viscera and the portion of the alimentary canal visible.
- FIG. 3. Relative position of the alimentary canal including the Malpighian tubules, in the body of the insect. (Complete fore-gut not shown.)
- FIG. 4. Longitudinal section through the head and fore-gut. The fore-gut is extremely short and the anterior end is marked by the powerful mandibles and molar crushing surfaces.
- FIG. 5. Cross-section through a portion of the fore-gut. The thick layer of circular muscles is most evident in this section.
- FIG. 6. Longitudinal section through the oesophageal valve. The spiny character of the fore-gut, the proventriculus, the flaps of the valve, the crossing of the longitudinal muscles from the fore-gut to the mid-gut and the circular muscle bands causing the ringed appearance of the mid-gut, are structures emphasized in this figure.
- FIG. 7. Diagrammatic sketch showing the flaps or folds of the oesophageal valve.
- FIG. 8. Diagrammatic sketch showing the relation of circular and longitudinal muscles at the anterior end of the mid-gut.

## PLATE II.

- FIG. 9. Diagrammatic sketch showing ramifications of the tracheoles throughout the muscles in the walls of the mid-gut.
- FIG. 10. Cross-section through a portion of the wall of the mid-gut. The nuclei fade out near the distal ends of the digestive cells, which are ruptured, allowing their secretions to be poured out into the lumen of the mid-gut. A heavy infestation of parasites occurs in the epithelium.
- FIG. 11. Longitudinal-section through the pyloric valve, showing the nature of the valve and the abrupt transition from the mid-gut to the hind-gut. A Malpighian tubule is seen entering the lumen of the alimentary canal just anterior to the commencement of the chitinous intima of the hind-gut.
- FIG. 12. Cross-section through the hind-gut in the region of the colon. The six strong bands of longitudinal muscles are illustrated, with the Malpighian tubules between them. The flattened character of the epithelium is noticeable.
- FIG. 13. Longitudinal-section through the union of the hind-gut and the rectum. This sketch shows the thick layer of circular muscles in the anterior end of the rectum and the abrupt transition between the two regions.
- FIG. 14. Cross-section through the rectum illustrating the rectal pads.
- FIG. 15. Cross-section through a rectal pad. The surface of the pad is very convoluted and powerful circular muscles underly the epithelium.
- FIG. 16. Longitudinal-section of a Malpighian tubule showing the large nucleus and concretions of waste products.
- FIG. 17. Cross-section through a Malpighian tubule near its union with the alimentary canal at the pyloric valve.
- FIG. 18. Cross-section through a Malpighian tubule near its attachment to the hind-gut.
- FIG. 19. A diagrammatic sketch of the peculiar band-like arrangement of the Malpighian tubules at the point of attachment to the walls of the hind-gut.
- FIG. 20. Diagrammatic sketch illustrating the arrangement of the longitudinal muscle bands and the Malpighian tubules on the wall of the colon.
- FIG. 21. Diagrammatic sketch showing the blind ending of a Malpighian tubule near the rectum.

## ABBREVIATIONS USED IN THE FIGURES.

AB.....	Abdomen.	MG.....	Mid-gut.
BC.....	Buccal cavity.	MS.....	Molar surface.
BM.....	Basement membrane.	MT.....	Malpighian tubule.
BR.....	Brain.	N.....	Nucleus.
C.....	Colon.	NID.....	Nidus.
CM.....	Circular muscles.	OE.....	Oesophagus.
CMB.....	Circular muscle bundles.	OUF.....	Oesophageal valve flaps.
CNS.....	Concretions.	OV.....	Oesophageal valve.
CT.....	Connective tissue.	P.....	Pharynx.
E.....	Epithelium.	PAR.....	Parasite.
FG.....	Fore-gut.	P INT....	Primary intima.
HD.....	Head.	PM.....	Peritrophic membrane.
HG.....	Hind-gut.	PV.....	Proventriculus.
HP.....	Hypopharynx.	R.....	Rectum.
IL.....	Ileum.	RO.....	Reproductive organs.
INT.....	Intima.	S INT....	Secondary intima.
LBI.....	Labium.	SP.....	Spines.
LBR.....	Labrum.	T.....	Testes.
LM.....	Longitudinal muscles.	TH.....	Thorax.
LN.....	Lumen.	TR.....	Tracheoles.
MD.....	Mandible.	1, 2, 3, 4, 5.	Abdominal segments.



